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HEREDITY OF SKIN PIGMENT IN MAN. II

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E. INHERITANCE OF ALBINISM

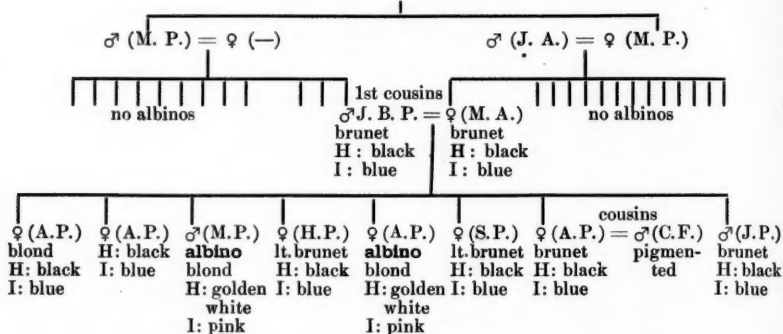
Albinism is the absence of pigmentation through lack of either, or both, the chromogen and the oxidizing ferment. The condition occurs widespread among animals and plants. In man it is rather rare, probably not occurring (if one may hazard a mere guess) in the population of the United States, as a whole, in more than in one case in 10,000 people.

Of true albinism in man there are all degrees. Aside from the piebald condition occasionally found in colored persons there are various grades of uniform depigmentation—hair color varying from light yellow to pure white; irides varying from pale blue to absence of blue, and pupils varying in the intensity of the pink color. Indeed, there is abundant testimony that persons born as albinos may acquire a slight pigmentation. Such a case was cited by Dr. H. B. Young (1905) from Illinois. Albino cats also vary in the pinkish glow of the retina.

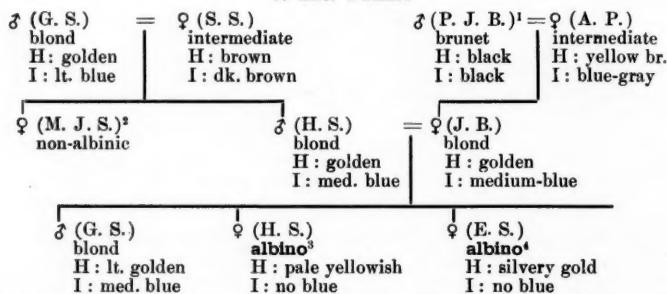
Despite variations in the completeness of depigmentation albinism can usually be clearly distinguished, at least in its more marked grades, and so we can study its inheritance. The cases given below were mostly col-

Note.—R. R. seen by me.

6. PAR. FAMILY

(b) *Albinos in Families with Suspected Consanguinity*

7. SAC. FAMILY

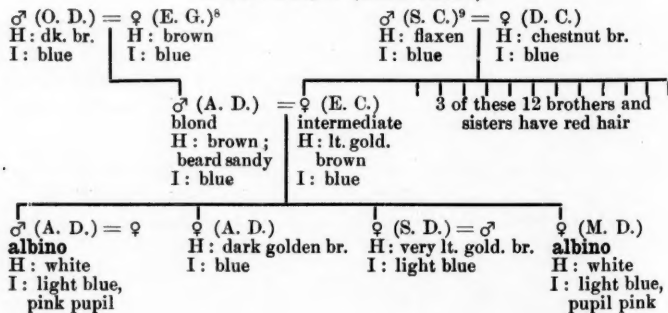


Note.—Seen by C. B. D. and S. E. ¹ and ² have the same middle name.

³ and ⁴ show reddish glow through pupil.

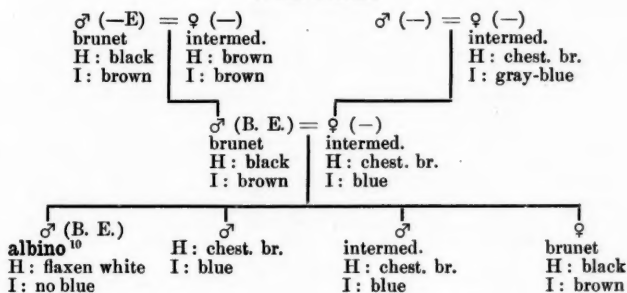
(c) *Albinos in Caucasian Families with no Evidence of Consanguinity*

8. DON. FAMILY (IRISH ORIGIN)



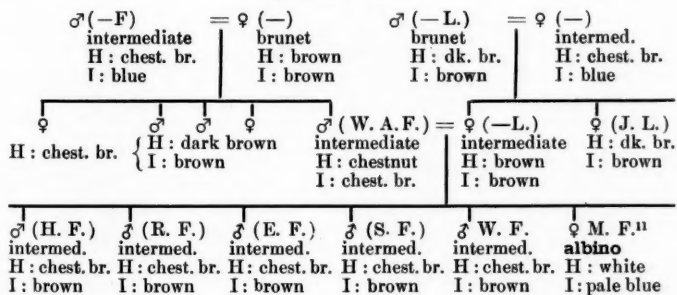
Note.—Seen by C. B. D. No relative on either side known to be an albino.

9. ED. FAMILY



Note.—Seen by S. E.

10. FAR. FAMILY



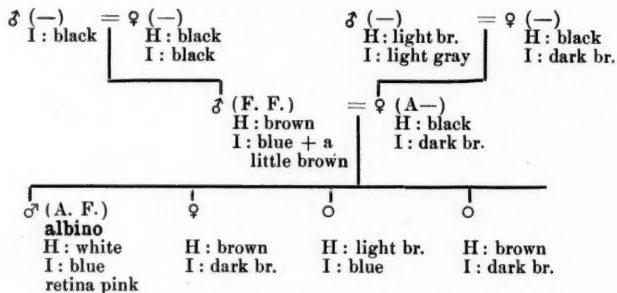
⁸ Some relatives with sandy hair.

⁹ Many of his relatives have red hair.

¹⁰ Hair white as snow; retina with bright pinkish glow; nystagmus moderate; shortsighted; can read 9 pt. Modern (Roman) type at three inches from eyes; school work middling. Red hair in ancestry, three generations back.

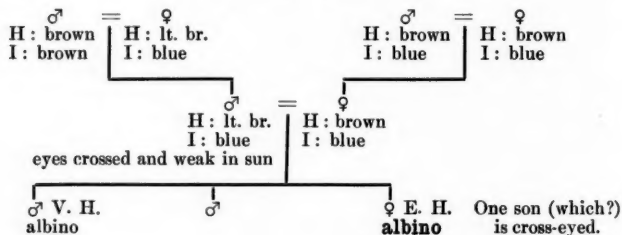
¹¹ Seen by S. E. Retina, medium pinkish glow; nystagmus slight; reads No. 9 Modern (Roman) print at nine inches; school work satisfactory. No consanguinity known.

11. FER. FAMILY (ITALIAN)

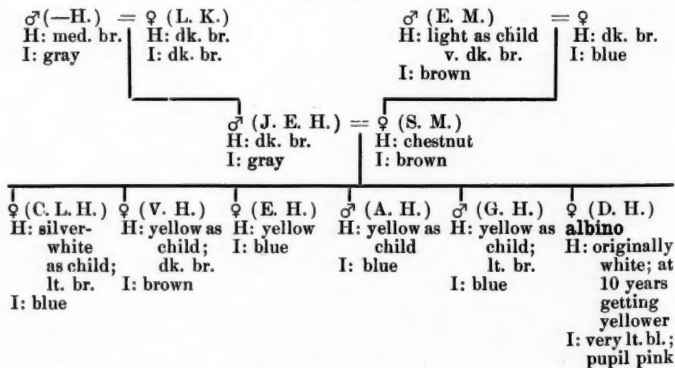


Note.—Seen by C. B. D. No consanguinity so far as known. No other albino relatives recalled.

11a. HLO. FAMILY (BOHEMIAN)



12. HOR. FAMILY



Seen by C. B. D. Nystagmus present.

♂ (—H.) = ♀ (—)		♂ (—) = ♀ (—)		♀
brunet		brunet		blond
H: black		H: brown		H: light
I: brown		I: brown		I: blue
♂ (—H.) = ♀ (—)		♂ (—) = ♀ (—)		
brunet		brunet		
H: black		H: black		
I: brown		I: brown		
♂ (B.H.) = ♀ (S.H.)		♂ (S.H.) = ♀		
brunet		brunet		
H: black		H: brown		
I: blue		I: brown		
♂ (S.H.) = ♀		♂ (S.H.) = ♀		
brunet		brunet		
H: dk. br.		H: dk. br.		
I: blue		I: brown		
♂ (S.H.) = ♀		♂ (S.H.) = ♀		
brunet		brunet		
H: dk. br.		H: dk. br.		
I: brown		I: brown		
♂ (M.H.) = ♀		♂ (I.H.) = ♀		
brunet		albino ¹²		
H: black		H: faint yel.		
I: black		I: med. blue		
♂ (I.H.) = ♀		♂ D.H. = ♀		
brunet		intermed.		
H: black		H: brown		
I: brown		I: brown		
♂ (S.H.) = ♀		♂ (S.H.) = ♀		
brunet		brunet		
H: dk. br.		H: dk. br.		
I: brown		I: brown		

Seen by S. E.

$\sigma^7 (-I_2)$ = ♀ (-) $\sigma^7 (-)$ = ♀ (-)
 blond intermed. brunet brunet
 H: flaxen H: brown H: brown
 I: blue I: brown I: brown

$\sigma^7 (I. L.)$ = ♀ (E. L.)
 blond brunet
 H: flaxen H: black
 I: blue-gray I: dk. br.

$\sigma^7 (B. L.)$
albino¹³
 H: white
 I: pale blue

Seen by S. E.

♂ (P. M.) = ♀
 interm.
 H: brown
 I: lt. br.

♂ (P. M.) = ♀ (A. M.)
 blond
 H: lt. br.
 I: lt. blue

♂
albino¹⁴
 H: white
 I: blue-gray

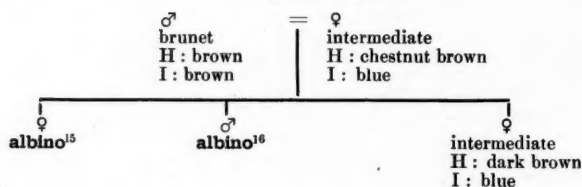
Seen by S. E.

¹² Retina with slight pinkish glow; nystagmus present in moderate degree; congenital hypermetropia.

¹⁸ Retina pigmented; nystagmus present; nearsighted.

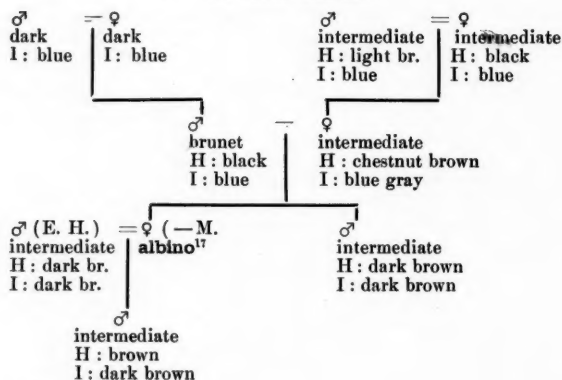
¹⁴ Retina pinkish; nystagmus present; very slight internal strabismus; general intelligence; average at school work, reads readily; sight good except in bright light.

16. MCK. FAMILY



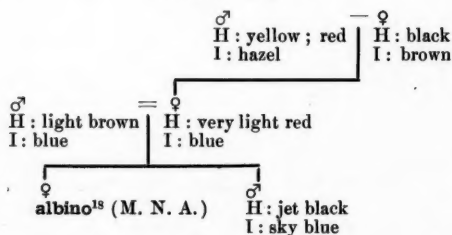
Seen by S. E.

17. MOO. FAMILY



Seen by S. E.

18. NEA. FAMILY



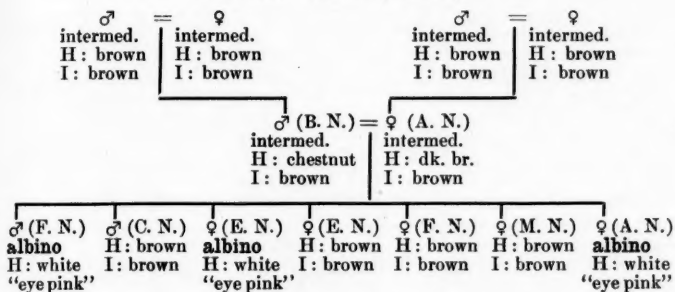
¹⁵ Hair white; iris pale blue; retina pinkish as seen through pupil; nystagmus present; slight internal strabismus; work at school very difficult, sight growing weaker.

¹⁶ Details as above. Eyes stronger, can read No. 9 point at 18 inches.

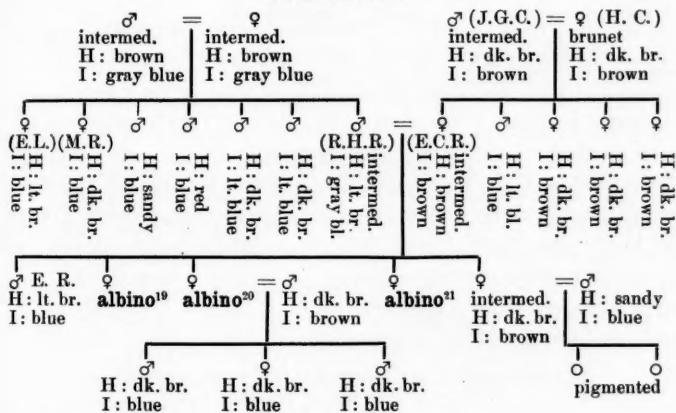
¹⁷ Hair white; iris light blue, retina dark (almost black), nystagmus present, has congenital high degree of myopia. Fairly good at school, can see to sew at night, bright in conversation.

¹⁸ Complexion very fair, hair white, iris clear blue.

19. NOG. FAMILY (ITALIAN)

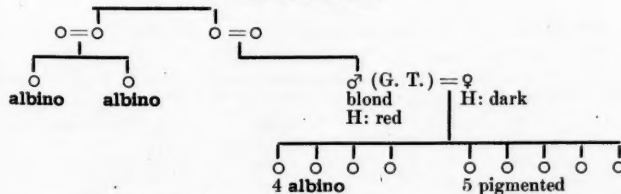


20. RID. FAMILY



Seen by S. E.

21. THO. FAMILY

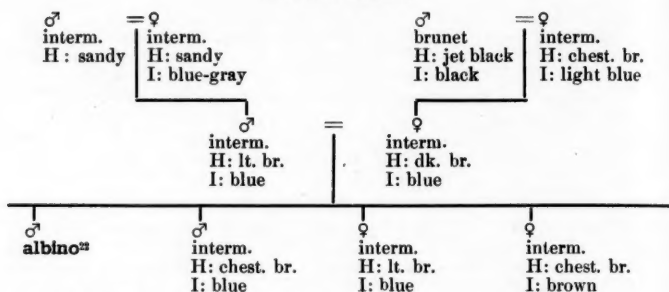


¹⁹ Hair, faintly yellowish; iris, devoid of blue; retina with medium pinkish glow; nystagmus moderate; myopia, school work satisfactory; read a good deal; sparetime spent in weaving seats of cane chairs.

²⁰ Hair faintly yellowish; iris devoid of blue; retina with medium pinkish glow; nystagmus moderate; myopia; school work middling.

²¹ Hair faintly yellowish; iris pale blue; retina with medium pinkish glow; nystagmus moderate; myopia; school work middling.

22. WIL. FAMILY

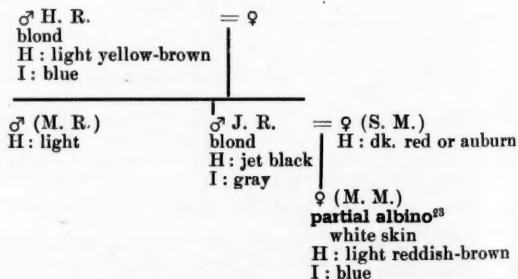


Seen by S. E.

23. The P-W family. The relationships of the members of this family, so far as worked out, are shown in the diagrams 23a, 23b, 23c and 23d. The persons in these diagrams come from the same general region and several surnames are common, especially those indicated by the initials P and W. The frequent recurrence of the same four surnames in the paternal and maternal sides of the ancestry of most of these albinos is testimony to a wide spread consanguinity. Further details are reserved for a later paper when it is hoped the pedigrees can be extended and connected.

(d) Colored Families

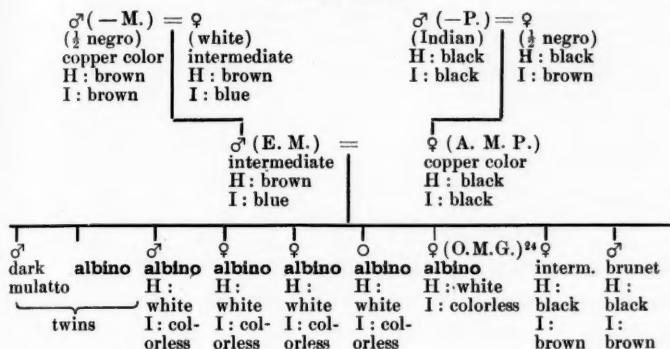
24. MER. FAMILY



²² Hair white; iris pale blue; retina bright pink; nystagmus marked; eyes sensitive to bright light, sees better in half light. "Kept up with the rest in school."

²³ Seen by C. B. D. Retina not pink. Slight nystagmus.

25. MAN. FAMILY



Seen by S. E.

25. Under this head may be cited the observations of Dr. Hrdlicka, who has collected data concerning ten albino Hopi Indians and two albino Zuni.

It appears from his data that "albinos marry full-colored individuals of the opposite sex. They seldom raise any children and never have large families of their own." All of the albinos whose data follow have a pinkish-white skin and gray-blue or blue eyes. The color of hair varies from flaxen to light brown.

A summary of the data relating to inheritance of albinism is given in Tables A and B.

TABLE A

GIVING THE COLOR CONDITION OF THE FRATERNITY OF EACH ALBINO DESCRIBED. THE PARENTS ARE, IN ALL CASES, OF NORMAL COLOR.

No.	Sex.	Number of Fraternity.		No.	Sex.	Number of Fraternity.	
		Normal.	Albinic.			Normal.	Albinic.
1	φ	2+?	1	7	φ	4 or 5	1
2	φ	1+!	1	8	φ	2	1
3	φ	2	1	9	φ	1	1
4	σ^8	3	1	10	σ^8	3	1
5	σ^8	4	1	11	σ^8	7	1
6	φ	4	2	12	σ^8	4	2
Total				37+ or 38+			

²⁴ Retina pinkish; nystagmus present; myopic; can read nine point print at five inches.

TABLE B

GIVING THE NUMBER OF NORMAL AND OF ALBINIC OFFSPRING OF AN ALBINIC INDIVIDUAL MARRIED TO A NORMAL.

N, normal; A, albinic, D, the dominant character; R, the recessive.

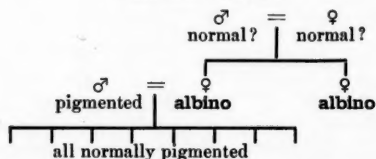
D	R	DR (=N)	RR (=A)
N ♀	A 4 ♂ ²⁵	0	0
N ♂	A 7 ♀	0	0
N ♂	A 9 ♀	1	0
N ♀	A 11 ♂	1	0
		2	0

If we consider *both* parents of the fourteen albinos listed in Table A as simplex in pigment, *i. e.*, as having not only normal but also albinic germ-cells, they were "DR's." When two such simplex (DR) individuals are mated, we expect 25 per cent. of the offspring to be duplex (DD), 50 per cent. simplex (DR or RD), and 25 per cent. without pigment (RR). Only the last will be albinic, 75 per cent. will be of normal color. We actually find that with fourteen albinos there are associated in their fraternities 37 + or 38 + normal individuals, expectation being 42. The deficiency would doubtless be accounted for by the unincorporated normal children. Since the proportion of albinic offspring in the given fraternities accords with expectation on the assumption that albinism is recessive that assumption is justified.

Second, if albinism is recessive, it should not appear in offspring of albinos with normal consorts. Unfortunately the sterility of the cross makes it difficult to get the desired data, but so far as they go, they are not in disaccord with hypothesis.

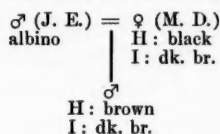
III. ONE PARENT ALBINIC

26. EDD. FAMILY

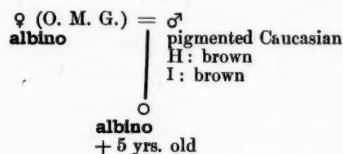


²⁵ These numbers refer to the serial numbers of the cases as given in Table A.

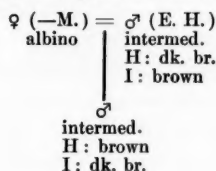
27. ENN. FAMILY (CONTINUATION OF No. 5)



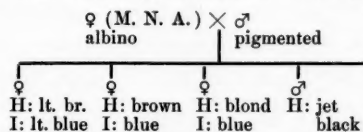
28. MAN. FAMILY (CONTINUATION OF No. 24)



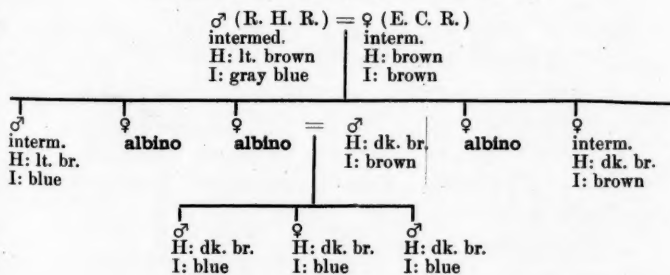
29. MOO. FAMILY (CONTINUATION OF No. 17)



30. NEA. FAMILY (CONTINUATION OF No. 18)



31. RID. FAMILY (CONTINUATION OF No. 20)



IV. THE D. G. V. FAMILY (see Plate)

This remarkable family comprises a great mixture of white, negro and even Indian blood, as well as many consanguineous marriages. The MAN family comes from the same rural community, but its connections with the D. G. V. family have not yet been established. It will be observed that every albino has the blood of all three families D., G. and V., so it can not be said, at present, from which family albinism originally came. It will be noted, also, that both of the youngest family (whose history is best known) arise from cousin marriages. Considering only those families in which albinism actually occurs there are 8 albinos in 22 children, which is a greater proportion than the expected 25 per cent. (5 or 6 albinic offspring). It is clear, however, that it may well be that there is potential albinism in one or more of the families with 3 to 5 children, in which by chance it fails to appear—the 22 children are merely a minimum.

Details about some of the persons in this family follow:

V.¹ 7, Yellowish complexion, brown hair and iris.

V. 8, Yellowish complexion, light brown hair, blue iris.

V. 9, An almost white mulatto, very light brown hair, blue iris.

V. 10, An almost white mulatto, brown hair, blue iris.

VI. 4, Intermediate complexion, light brown hair, gray iris.

VI. 5, Yellowish complexion, light brown hair, blue iris.

VII. 1, T. V., aged 3, albino, hair white, iris colorless, retina with pinkish glow, nystagmus present, intellectually bright and well developed.

VII. 2, F. V., aged 4, intermediate complexion, hair and iris dark brown.

VII. 3, M. V., aged 1, brunet, hair and iris black.

V. 20, J. V. (Indian, French and negro blood), yellow skin, very light brown hair, yellow iris.

^{23a} The Roman numeral refers to the generation; the Arabic to the individual.

TABLE IX
SHOWING THE HAIR AND EYE COLOR OF PARENTS AND GRANDPARENTS OF ALBINOS ARISING FROM PIGMENTED PARENTS

No.	Name.	Father.		Mother.		F.F.		F.M.		M.F.		M.M.	
		Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye.	Hair.	Eye.
4.	She.	br	br	dk.br	br	br	br	yell.br	bl	N	br	lt.br	bl.
5.	Eun.	N+R	br	dk.br	dk.br	lt.yell.br.	dk.bl	N	dk.br	yell.br	lt.br	N	dk.br
7.	Sac.	gold	bl	bl	bl	gold	lt.bl	br	dk.br	N	N	yell.br	bl.gr
7a.	Bro.-7	dk.br	N	bl	bl	—	—	—	—	—	—	—	—
8.	Don	br+R	bl	lt.goldbr.	bl	dk.br	bl	br	bl	flax	bl	chest.br	bl
9.	Ed.	N	br	chest.br	bl	N	br	br	br	—	—	chest.br	gray bl
10.	Far.	chest	chest.br	br	br	chest.br	bl	br	br	dk.br	br	chest.br	bl
11.	Fer.	bl	bl	dk.br	dk.br	N	—	N	N	lt.gray	lt.gray	chest.br	dk.br
11a.	Hio.	br	bl	bl	bl	br	lt.br	br	br	br	bl	br	bl
12.	Hor.	dk.br	gray	chest	br	br	gray	dk.br	dk.br	lt. to dr.br	br	dk.br	bl
13.	Hut.	br	br	dk.br	br	N	br'	br	br	br	br	yell.	bl
14.	Lie.	flax	bl.gray	N	dk.br	flax	bl	br	br	br	br	br	br
15.	Meg.	lt.br	lt.bl	chest.br	chest.br	br	lt.br	br	lt.br	—	—	—	—
16.	Mek.	br	br	chest.br	bl	—	—	—	—	—	—	—	—
17.	Moo.	N	bl	chest.br	bl.gray	—	bl	—	bl	lt.br	bl	N	bl
18.	Nea.	lt.br	bl	v. lt. red	bl	—	—	—	—	yell.red	hazel	N	br
19.	Nog.	chest	br	dk.br	br	light	br	br	br	light	br	N	br
19a.	Pit.	N	N	dk.br	bl	br	blue	N	N	dk.br	br	N	br
20.	Rid.	lt.br	gray bl	br	gray bl	br	gray bl	—	gray bl	—	—	dk.br	br
21.	Tho.	red	—	dark	—	—	—	—	—	—	—	—	—
22.	Wil.	lt.br	bl	dk.br	bl	sandy	—	sandy	bl.gray	N	N	chest.br	lt.bl

V. 21, M. (Irish origin), brunet, black hair, blue iris.

VI. 10, J. V., Brunet, brown hair, blue iris.

VI. 11, S. G., Intermediate complexion, brown hair and iris.

VII. 15, A. V., Aged 18, albino, white hair, colorless iris, retina pinkish, nystagmus present, mentally quick.

VII. 18, L. V., Aged 24, albino, white hair, colorless iris.

V. THE CONDITION OF HAIR AND EYE COLOR IN THE PIGMENTED PARENTS OF ALBINOS

Assuming all pigmented parents of albinos to be simplex in pigment we may inquire if such simplex parents differ from the population at large in their hair and eye color. To get an answer to this inquiry Table IX has been drawn up.

This table is summarized in Table X, so as to bring out the relative frequency of the different types.

TABLE X

THE RELATIVE FREQUENCY OF THE DIFFERENT TYPES OF HAIR AND EYE COLOR IN THE PARENTAGE OF ALBINOS

Hair Color.							Eye Color.								
Types.	F.	M.	FF.	FM.	MF.	MM.	Total.	Types.	F.	M.	FF.	FM.	MF.	MM.	Total.
N (black)	3	2	3	3	3	5	19	N (black)	2			2	2		6
dk. br.	2	8	1	1	2	2	16	dk. br.		3		3		2	8
br.	5	3	6	10	4	3	31	br.	6	6	4	5	7	5	32
lt. br.	4				2	1	7	lt. br.			2	1	1		4
golden	1	2	2	1	1	1	8	chest. br.	1	1					2
yellow						1	1	hazel					1		1
flaxen	1		1		1		3	gray	1		1		1		3
red+N	1	1					2	blue-gray	2	1	1	2		2	8
red+dk.br.	1						1	blue	7	9	6	4	4	7	37
chestnut	2	4	1			3	10	lt. blue	1		1			1	3
red	1	1			1		3								
Total	21	21	14	15	14	16	101	Total	20	20	15	17	16	17	105

If Table X be compared with the proportional distribution of the different types of hair color in the population at large, certain differences are seen. Thus while black, dark brown and brown hair constitute in a random

population (Holmes and Loomis, 1909, p. 55) 695 out of 853 persons, or 81.5 per cent., in Table X, they constitute only 65 per cent. On the other hand, while, according to Holmes and Loomis (1909, Table III), red and auburn constitute only about 5.5 per cent. of their population, the various forms of red constitute 16 per cent. of the population of Table X, or three times the typical proportion. It appears then that, on the whole, the pigmented ancestry of albinos shows an excess of red and the weaker grades of melanic pigment.

The distribution of eye color, on the other hand, shows little that is abnormal. The "blacks" are somewhat deficient, about 70 per cent. as abundant as in the population as a whole, the browns are in excess, and the blues occur in nearly normal proportions. The last result was hardly anticipated as it might have been expected that the pale blue iris of the albino would be specially apt to proceed from blue-eyed parents, but this is not so. As a matter of fact, dark brown eyes are quite compatible with recessive albinism as Table XI shows. The general teaching of Table XI is that the heterozygous or simplex pigmentation of the offspring is not always clearly less than that of the darker parent. But, on the whole, blue iris predominates slightly and the hair tends to run

TABLE XI

SHOWING THE HAIR AND IRIS COLOR OF THE OFFSPRING OF AN ALBINO AND A PIGMENTED PARENT

Family.	Parents.			Offspring.	
	Albino.	Pigmented Parent.		Hair Color.	Iris Color.
		Hair Color.	Iris Color.		
Enn.	♂	N	dk. br.	br	dk. br.
Moo.	♀	dk. br.	dk. br.	br.	dk. br.
Nea	♀	pigmented	pigmented	lt. br.	lt. br.
				br.	blue
				blond	blue
				jet black	—
Rid.	♀	dk. br.	br.	dk. br.	blue
				dk. br.	blue
				dk. br.	blue

lighter than, or at least not to exceed, that of the darker parent.

VI. THE ORIGIN AND "CAUSE" OF ALBINISM

The question remains to be discussed: What is the origin and "cause" of these albinos. The general conclusion seems justified, as in other mammals so in man, albinism is due to the fortuitous union of two germ-cells lacking this factor so that it is absent in the zygote whence the albino proceeds.

The objections to this view are three: (1) The usual absence of any history of albinism in the family; (2) the improbability of so frequent unions of two persons bearing albinism recessive; (3) the lack of statistical accord of the results of human breeding with those of animals.

The first objection is not valid for any one who has done experimental breeding, because he knows full well how the recessive condition may be carried unexpressed in the germ-cells for many generations awaiting that chance conjugant that also carries the recessive condition. Absence of any history of albinism in a family has the less significance in a country like ours where a large proportion of the population can not tell the names of their grandparents and know little of their cousins, who may, indeed, live one to three thousand miles away.

The improbability of so frequent unions of two or three persons having albinism recessive has been referred to by Pearson. With a mathematical showing, he tells the story of an albino who married successively two pigmented (?) husbands and had some albino children by each. "All three stocks, according to Mendelian hypothesis, ought to have albinism in a recessive form. You can calculate the chances against that because an albino occurs in Italy about 1 in 30,000, in Norway, about 1 every 20,000 of the population, in Scotland, 1 in 24,000. What are the chances that a woman of albinotic stock should marry two stocks affected with albinism and not related either to her or to each other?" The inference

seems to be that Pearson would be content with "calculating the chances" and, because the ratio was small, insisting that the three stocks could not all have albinism recessive. Such a method of procedure is, I fear, all too characteristic of the "careful work" which alone, according to its editor, is admitted to the pages of *Biometrika*.²⁶ Of course the facts are that we have here no data for calculating the required chances. In the first place, the term "not related" has only a relative significance in the statistics of human qualities; it usually means not first cousin or nearer relative, more rarely extends to second cousin, or at the outside, to third cousin. And yet two persons of the grade of tenth cousin may easily carry recessive an albinic condition derived from a common source. A fairer question would be, what are the chances that a woman shall marry in succession two men related between the grades of third and tenth cousin, supposing, further, all three come from the same rural district, long settled and relatively stable? I think the conditions that Pearson does not cite might easily render the chances several million to one in favor of the three persons being less distantly related than tenth cousin. An actual illustration of this condition of affairs is shown in the D. G. V. and P. W. families. The three family names represented by D., G. and V. occur again and again in this family, as the pedigree table shows. Some of the consorts are recognized as "first cousins"; but in most other cases they are stated to be "unrelated." If the inquiry is pressed the admission is made "were perhaps *distantly*." One may "calculate the chances" that in the same mountain community, of perhaps 300 inhabitants, who are all segregated by color from the surrounding population, two persons of the same name (uncommon outside the community) are absolutely *unrelated*, or unrelated outside the degree of seventh cousin. But even in a flat

²⁶ In justice it should be added that the remark was not made in *Biometrika*.

country, penetrated by a railroad, we find, as in the P. W. family, a large proportion of consanguineous marriages. The argument against the probability of unions with recessive albinism has not yet been presented with any force.

The third point—the lack of statistical accord between the results of human breeding and those of animals—has been often remarked upon. Bateson (1909, p. 28, footnote) believes the descent of albinism in man to be complicated by some unascertained disturbance. A careful consideration and analysis of the statistics indicates, I think, that this disturbance is to be found in the method of collecting the statistics. From the matings of two persons that are simplex in pigmentation, two sorts of families are to be expected, namely, those with albinos and those without. Since in the long run, from such parents, only one albino is produced in four offspring, it is clear that the chances are that in all families of one,

TABLE XII

GIVING ALL FAMILIES CONTAINING ALBINO OFFSPRING FROM TWO PIGMENTED CAUCASIAN PARENTS

Reference.	Offspring.				Reference.	Offspring.			
	Albinic.	Pigmented.	Total.	Per Cent. Albinic.		Albinic.	Pigmented.	Total.	Per Cent. Albinic.
She.	1	3	4	25	Tho.	4	4	9	60
Enn.	7	7	14	50	Wil.	1	3	4	25
Sac.	2	1	3	67	P-W.a.	1	11	12	8
Don.	2	2	4	50	P-W.a. III. 15	5	3	8	62
Ed.	1	3	4	25	P-W.b. II. 2	2	7	9	22
Far.	1	5	6	17	P-W.b. IV. 3	1	2	3	33
Fer.	1	3	4	25	P-W.c. I. 1	1	0	1	—
Hlo.	2	1	3	67	P-W. VI. 1	1	3	4	25
Hor.	1	5	6	17	P-Wd. III. 11	1	0	1	—
Huf.	1	5	6	17	P-W. IV. 1	1	12	13	7
Lie.	1	0	1	—	D.G.V. II. 1	4	1	5	80
McG.	1	0	1	—	D.G.V. IV. 5	1	2	3	33
McK.	2	1	3	67	D.G.V. VI. 10	2	8	10	20
Moo.	1	1	2	50	D.G.V. V. 24	1	3	4	25
Nea.	1	1	2	50	Men.	1	0	1	—
Nog.	3	4	7	42	Man.	6	3	9	67
Ria.	3	2	5	60					
					Totals.	64	107	171	374

two or three children albinism will not appear. Even in families of four or more the possible case of albinism may fail to occur. All such cases of an actual low ratio of albinism are omitted from any calculation of proportions; chiefly the accidentally high ratios are brought under consideration. The actual proportions of albinos to all offspring of two pigmented parents are given for each family in Table XII.

These 33 families together with two not plotted in the diagrams are summarized in Table XII.

TABLE XIII

THE PROPORTION OF ALBINOS IN ALBINIC FAMILIES OF DIFFERENT SIZES,
WHEN NEITHER PARENT IS ALBINIC

No. of Children in Family.	No. Albinic.	Per Cent. Albinism.	Families.	Total Number of Families.
1	1	100	Lie., Mcg., P.W. (bis)	4
2	1	50	Moo., Nea.	2
3	2	67	Sac., Mck.	2
3	1	33	Vin., D.G.V., P.W.	3
4	2	50	Don.	1
4	1	25	She., Ed., Fer., Gur., Wil., D.G.V., P.W.	7
5	4	80	D.G.V.	1
5	3	60	Ria.	1
6	2	33	Wes.A.	1
6	1	17	For., Hor., Huf.	3
7	1	14	P.W. (not platted)	1
7	3	42	Nog.	1
8	5	63	P.W.	1
9	6	67	Man.	1
9	4	44	Tho.	1
9	2	22	P.W.	1
10	2	20	D.G.V.	1
12	1	8	P.W.	1
13	7	54	Enn.	1
13	1	8	P.W.	1
				35

Taking Table XIII in its entirety there is an average of 44 per cent. albinos to a family where expectation is 25. If we consider only the families with four or more children we find the average proportion of albinos to be 34 per cent. If we take families with six or more children the average proportion of albinos falls to 32 per

cent.; with 10 or more children to 23 per cent. On the average, with the larger families the proportion of albinos tends to approach expectation.

A second source of error is not to be neglected. When the attention of the parent or acquaintance is focused by the questioner upon albinos the albinic children are all recalled, while some normal children (such as were still-born or died in infancy) are more apt to be forgotten. I have repeatedly had the experience of bringing to mind by further questioning children that had not been at first mentioned, and they were always normal children. The records of families with only one child and that an albino are frequently due to the fact that the peculiar child is the only one recalled. Considering the high frequency of infant mortality the omission of normal children forms an important factor tending to raise the proportion of albinos.

A third possible source of error lies in imperfection of dominance, *i. e.*, the occasional failure of the pigment to show itself in the young children who have it simplex. Of this imperfection there are all degrees. Thus the albinos in the LIE (No. 14) and Moo (No. 17) families have a dark retina with white hair, washed-out blue iris and nystagmus. In other cases, such as the Rm family (No. 20) and P-W,_A (XII, 24, 25), the hair is yellowish, while the retina is pink, or the pinkish retinal glow and nystagmus may be slight. Another fact that favors the view of frequent failure of the simplex determiner to activate fully is the progressive increase in pigmentation shown by some albinos. This is a common phenomenon. Seligsohn in Eulenburg's "Real Encyclopädie," 1880, p. 162, states: "Bei einem vorgesunden Eltern mit allen Merkmalen einer Albino geborenen Kinde schwand die rothe Farbe der Iris von Jahr zu Jahr." This increase in development of a simplex character has been observed by Lang in snails, by one of us in poultry and by others.

In concluding this discussion of the causes of the aberration in the proportion of albinos I wish to urge that

what is needed in these studies is not so much a vaster number of families as more families that have been completely and accurately studied. Human pedigrees, like breeding records, are full of imperfect statements. The whole truth is to be gained only by visiting the families and carefully cross questioning them.

VII. CONCLUSIONS

What conclusions can be drawn from a study of the foregoing study of albinos?

1. Two albinic parents have only albinic offspring. This holds for the families Nos. 1-3, comprising four children altogether. These cases were all given us by Mr. R. R., an intelligent and reliable albino. He married an albino and had one son still, or until recently, living; albinic like his parents. These cases are, so far as I know, the first that have been published.

Dr. R. A. Gortner tells us that he formerly knew of a family of two albino parents and five albino children near his home in Nebraska, but attempts to trace this family have proved unsuccessful. The probability that this rule will hold generally is enhanced from experiments on animals where two albinos always yield only albino offspring.

2. Even when neither parent of albinos is an albino they are apt to be related. In 33 such families 11 are almost certainly from consanguineous matings. This is 33 per cent., a proportion that is certainly vastly greater than that of the population at large.²⁷ The fact that consanguinity even when present must frequently be unknown heightens the probability that parents of albinos are usually related. The importance of this conclusion is that it tends to bring these cases under the general rule that a recessive condition appears only when both parents carry the same defect; and the probability that both carry the same defect is heightened when both belong to the same strain.

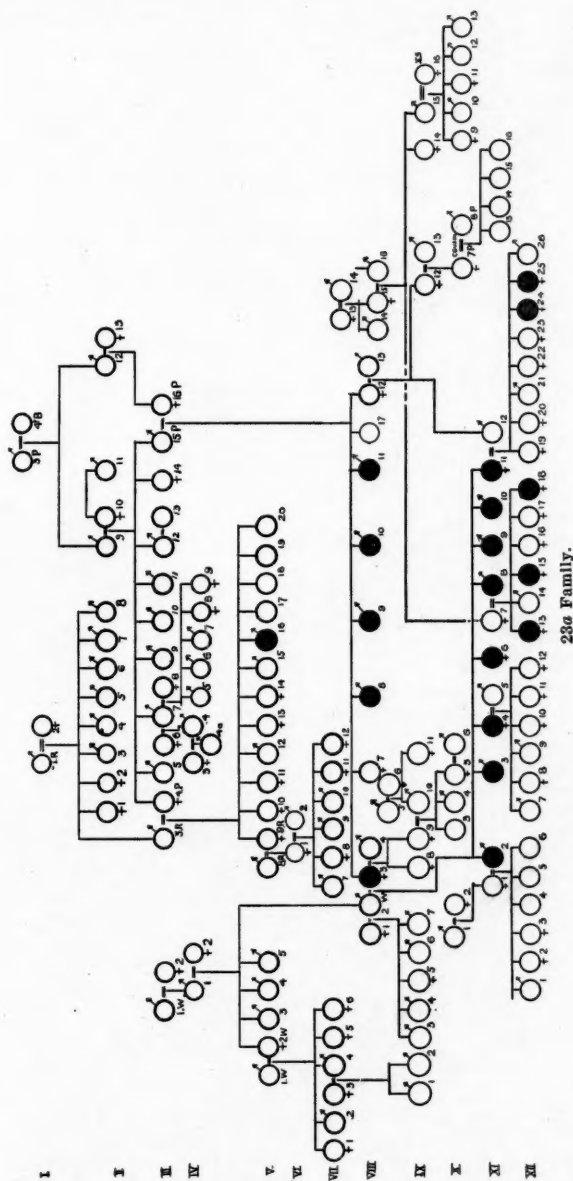
²⁷ Lagleyze (1907) finds in 48 families of albinos consanguinity in 10, with collateral antecedents in 7, non-consanguinity in 26, and unknown 5.

3. The proportion of albinos in any family probably accords in the long run with Mendelian expectation, as in other mammals. From two non-albinic parents the proportion for families of four or more children is 34 per cent. albinos instead of the expected 25 per cent. But various causes result in an omission of normal individuals and tend to swell the proportion of the abnormal. When one parent is albinic and albino offspring occur at all we get (RIL and 4 cases in P. W.), a total of 16 albinos and 15 pigmented, which accords with expectation.

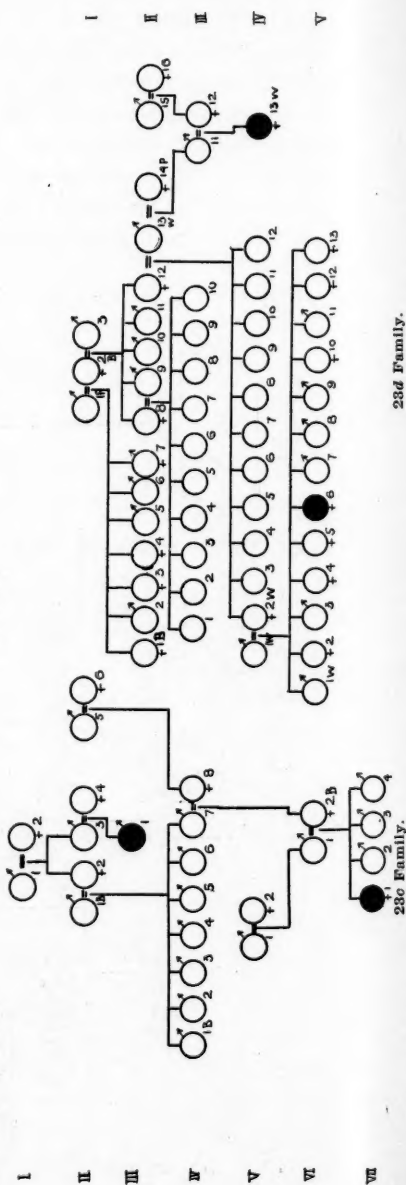
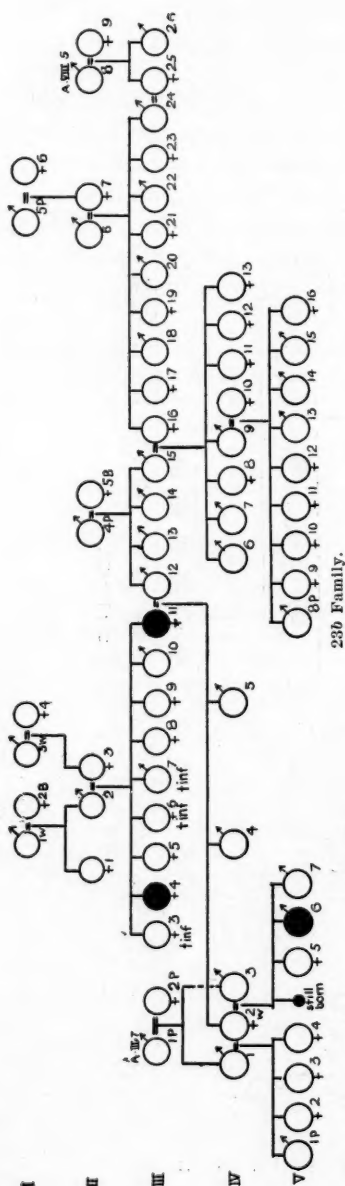
STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, N. Y.,
September 8, 1910.

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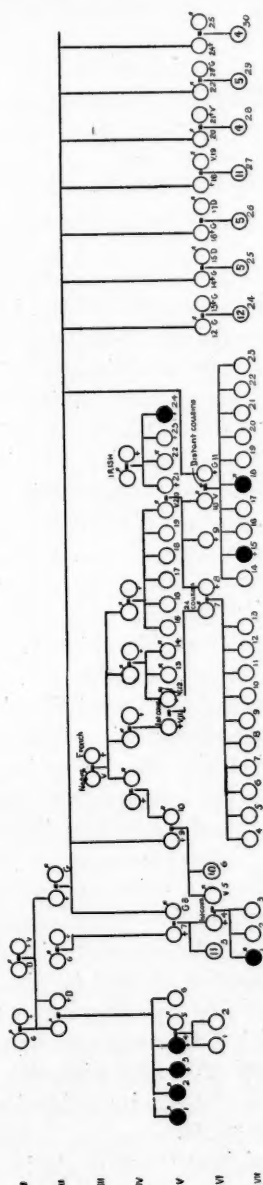
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23rd Family.



23d Family.



D. G. V. Family

SPAWN AND LARVA OF AMBYSTOMA JEFFERSONIANUM

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SPAWN

AMONG the various accounts of the habits and spawn of *Ambystoma punctatum* occasional mention may be found of *Ambystoma jeffersonianum* but always in such connections as to suggest that *A. jeffersonianum* is by far the less common species in the locality. This along with the considerable similarity existing between the spawn of the two species may explain why no account of the spawn of *A. jeffersonianum* has as yet appeared. Descriptions of the spawn of *A. tigrinum* sufficient for distinguishing it from that of the other two species is given by B. G. Smith (1907).

In most localities near Toronto *A. punctatum* is a much more common species than *A. jeffersonianum*, however in one piece of woodland that is quite isolated from all the others examined, the former species is rarely to be found, while the latter is very abundant. This woodland contains four pools that last throughout the year, although they become heavily choked by vegetation during the late summer and autumn. The value of these pools as a collecting ground for spawn, *Branchippus*, etc., was discovered some years ago by my colleague, Dr. Huntsman and his observations on the *Ambystoma* spawn suggested to him the possibility of distinguishing in it two kinds. Later the writer also became familiar with this woodland in connection with observations on *Plethodon* and with the consent of Dr. Huntsman undertook also the investigation of the *Ambystoma* spawn of the pools.

The writer first visited these pools in spawning time

three years ago and found a small amount of spawn of a type already familiar to him for some years from its abundance in pools in other localities. But the greater amount was of a type that differed from this in the points detailed below. These two types have proved to be the *punctatum* type and the *jeffersonianum* type, respectively. The predominance of the latter subsequently found its explanation in the fact that 31 of the 33 individuals captured in the woodland since then have been of the latter species. It is impossible to determine accurately the proportions in which the two types of spawn occur, but estimating roughly, the *jeffersonianum* type is at least ten times as abundant as the other.

As will appear below, a small percentage of the eggs of *A. punctatum* will approach in size, or color, or mode of deposition—but rarely in more than one of these points at a time—the eggs of *A. jeffersonianum*. Consequently, the separation of the latter as a type when found in a pool where the *punctatum* spawn greatly predominates, is not an obvious thing. But when the proportions are reversed, as in the special pools mentioned, the distinction is most easily made. Observations in the field have agreed in all four seasons and have been supplemented by the capture of females just previous to egg-laying and comparison of mature ovarian eggs and eggs laid by them in the laboratory, with those obtained in the pools; and finally by the rearing in the laboratory of larvæ from the two types of spawn.

The points of difference in order of constancy are as follows:

1. *Size*.—The eggs of *A. jeffersonianum* are distinctly the smaller, the usual diameter being 2–2.25 mm.
2. *Color*.—The eggs of *A. jeffersonianum* are much the darker, the pigment being but little removed from a true black and covering a much larger proportion of the surface of the egg than in *A. punctatum*; even the lower surface is usually as dark as the upper surface of many of the eggs of the latter species.
3. *Time of Laying*.—The deposition of most of the

spawn by *A. jeffersonianum* precedes that by *A. punctatum* by a few days. It has been impossible to visit daily the pools where the spawn of *A. jeffersonianum* is most abundant, owing to their distance from the university; one pool much nearer has yielded a small amount of it and has provided more accurate although more scanty data. In general the deposition of the bulk of the *jeffersonianum* spawn coincides with that of the first *punctatum* spawn. Variations from this occur—for instance, this year the spawn in the single pool just mentioned followed the above rule, while in the group of four pools nearly all the *jeffersonianum* spawn had been deposited three days before any *punctatum* spawn appeared; and to complete the irregularity the last spawn of all to be deposited was that of *A. jeffersonianum*. It was in small quantity and probably all from one female. (These eggs and the larvæ from them were unusually small, the larvæ seemed vigorous, but could not be kept alive many days after their own supply of yolk was exhausted.) Another check on the time is furnished by the spawning of *Rana sylvatica*. This year—an unusually early season—the writer observed the first deposition of spawn in these pools by the wood-frog. It began at 10.30 A.M., March 31. Spawn of *A. jeffersonianum* had appeared seven days previously.

4. *Spawn-masses*.—The typical spawn mass of *A. jeffersonianum* is a small one, the number of eggs being usually about twenty; the extremes encountered have been small masses of jelly without any eggs and a mass containing forty-one. *A. punctatum* does indeed deposit masses of spawn containing as few eggs as this, but the number is usually much larger. The complement of ripe ovarian eggs carried by two females of average size was 128 and 161. These are probably representative numbers and indicate a rather smaller complement than that possessed by *A. punctatum*—130 to 225—(Wright and Allen, 1908) which in turn is much smaller than that of *A. tigrinum*—1,000 or more (Powers, 1907).

5. Hardly less characteristic than the small masses is

the manner in which they are frequently to be found attached in succession to long slender twigs, each mass being usually in contact with its neighbors. A sentence in one paper on *A. punctatum* (Wright, 1908), "one stem—had within a length of one and a half feet 14 bunches of eggs, 15–20 eggs to the bunch," reads very much like a description of spawn of *A. jeffersonianum*. Many stems so laden have been found each year in the special pools mentioned. The largest piece in Fig. 1 is a portion of one of them. The twigs selected by *A. jeffersonianum* are, as a rule, very slender. *A. punctatum* will make use of both stout and slender twigs indifferently, and no small quantity has been found attached to the margins of leaves and to grass, even in the presence of such twigs as are generally preferred. Eggs of *A. jeffersonianum* have not been found except attached to twigs or stems of water plants.

The low vitality of much of the spawn of *A. jeffersonianum* is a feature that has been noticed in each year. No accurate estimate of the proportion that dies has been made, but judged roughly by the conditions found in the pools it is probably not overstating the loss to say that three fourths of the eggs do not live to begin gastrulation. The same proportion of loss has occurred in spawn reared in the laboratory, while spawn of *A. punctatum* brought from the same pools a little later and kept under the same conditions has suffered practically no loss. The egg does not die, as a whole, but cells here and there precede, the others going on dividing as usual one or more times, only to die at last. The surface view of such an egg when death is complete shows an irregular mingling of minute cells with many others two or three times as great, and at intervals others even up to eight or ten times as great, in diameter. These dead eggs imbibe considerable water, and become very much larger than the living ones and under natural conditions are soon infected by fungi; but in the laboratory they have been kept for weeks and have remained free from it; showing that death has not been caused by a fungus that

only later becomes visible. All the eggs of a mass either die or develop properly; one or two of the eggs may prove exceptions to this, but whatever the defect may be it involves practically all the eggs of a bunch. Whether it may extend to all the eggs of a female it has not been possible to determine. This loss has also been observed in spawn of *A. jeffersonianum* from a second locality and is not likely to be due to any quality of the water, for in the pools of each locality spawn of *A. punctatum* has been found developing with very little loss, and that apparently due to infection by fungus. Neither can it be ascribed to low temperatures from early deposition, for the earliest is no more liable to die than that which comes later along with or after the spawn of *A. punctatum*.

LARVA

Spawn of *A. jeffersonianum* brought to the laboratory has been allowed to develop and the larvæ fed until the larger specimens had attained a length of 30-40 mm. In these it has been possible to detect a peculiarity of marking not present in similar larvæ of *A. punctatum*. This peculiarity consists of a massing of dark chromatophores into three or four spots placed in a row along each side of the mid-dorsal line, giving the animal, when viewed from above, the appearance of being banded (Fig. 2). Viewed from the side the same can be detected, but is less conspicuous (Fig. 3). Incipient banding is often indicated as soon as the chromatospheres are well differentiated (Fig. 4).

In looking over a large number of larvæ all gradations will be found between individuals in which the above shows distinctly and those in which it is impossible to detect it. For example, in 115 laboratory-reared larvæ examined at one time, 80 (69 per cent.) showed the distinctive marking. Of the balance, some individuals under different conditions showed it also (either extreme expansion or contraction of the chromatophores obscures the pattern), but some never did. Exact numbers for this division of the 31 per cent. are not available.

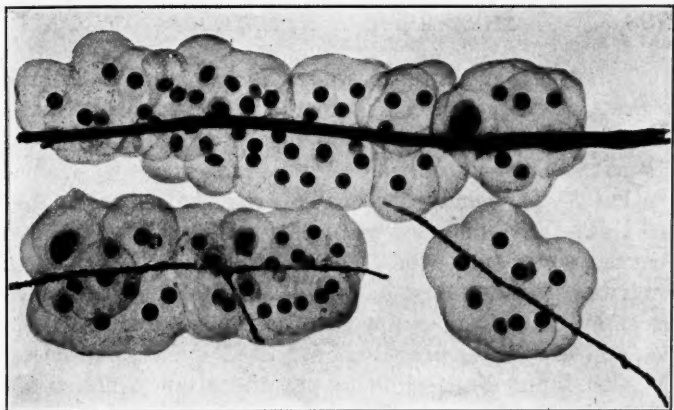


FIG. 1. Spawn of *A. jeffersonianum*. Natural size. The eggs of some of the masses are dead, others are in various stages from blastopore to medullary groove formation.



FIG. 2. Larvæ of *A. jeffersonianum*. Enlarged three diameters. Chromatophores considerably but not extremely contracted.

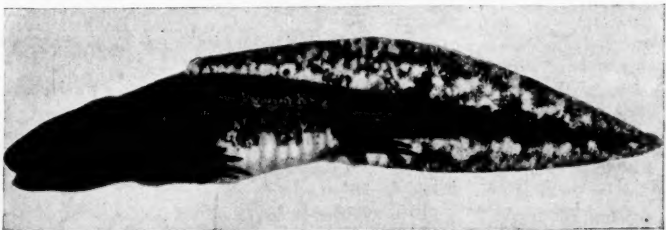


FIG. 3. Larva of *A. jeffersonianum*. Enlarged three diameters. Chromatophores considerably but not extremely expanded. The viscera and right side of the trunk have been dissected away and the photograph taken by both direct and transmitted light.



FIG. 4. Larva of *A. jeffersonianum*. Enlarged four diameters.

This year an attempt was made to remove all the spawn of *A. punctatum* from the special pools. In the middle of June larvæ 30-35 mm. long were collected from them and examined as to this pattern; it was found in but 35 per cent. Two causes may have contributed to this—the abundance of brush in the pools may have caused some spawn of *A. punctatum* to be overlooked, and the great expansion of the chromatophores—much greater than ever attained in the laboratory, the pools being very dark, probably disguised it in some cases. It was found impossible to put these larvæ under observation in the laboratory to test this point, for owing to the long journey or to the change of water they invariably died within a few hours.

Little importance would have been attached to a point of coloration so variable as this had it not been found to be uniformly lacking in similar larvæ of *A. punctatum*, whether raised in the laboratory or taken from the pools known to contain little, if any, spawn of *A. jeffersonianum*. In view of the range of coloration for *A. tigrinum* as larvæ (indicated by Powers), the degree of constancy noted is perhaps the most that could be expected.

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THE INHERITANCE OF SIZES AND SHAPES IN PLANTS

A PRELIMINARY NOTE¹

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SOME years ago Lock reported a cross of a tall race of maize with a shorter race which produced an intermediate height in F_1 and exhibited no segregation in F_2 when crossed back with one of the parents.² Castle's results with rabbits are very similar to those of Lock with maize. Castle summarizes his results in part as follows:³

A cross between rabbits differing in ear-length produces offspring with ears of intermediate length, varying about the mean of the parental ear-lengths. . . . A study of the offspring of the primary cross-breeds shows the blend of the parental characters to be permanent. No reappearance of the grand parental ear-lengths occurs in generation F_2 , nor are the individuals of that second generation as a rule more variable than those of the first generation of cross-breeds. . . . It seems probable that skeletal dimensions, and so proportions of skeletal parts, behave in general as blending characters. The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions.

From his own work with rabbits and Lock's work with maize, Castle offers this somewhat guarded generalization:⁴

It is probable that in plants, as well as in animals, linear dimensions are in general blending in their inheritance. . . . The obviously blending inheritance of height in this case [maize] does not contradict the known Mendelian behavior of the growth habit in such plants as the

¹ This paper was presented, in substance, in a lecture before the section of plant physiology of the Graduate School of Agriculture, Ames, Iowa, July 8, 1910. The complete records are to be published later by the Nebraska Agricultural Experiment Station.

² Lock, R. H., *Ann. Roy. Bot. Gard. Padova*, 3 (1906), p. 130.

³ Castle, W. E., et al., Carnegie Inst., Pub. No. 114 (1909), pp. 35, 43.

⁴ *Loc. cit.*, pp. 43, 44.

sweet pea. . . . Dwarfness is plainly such a discontinuous variation in plants as is hypophylangia in man, and its inheritance is quite different from that of ordinary variations in height. The former is a discontinuous variation, Mendelian in its inheritance; the latter belongs to a series of continuous variations, and is blending in its inheritance.

While, in case of most of the crosses that I have studied where the parents differ in size, the F_1 individuals show an intermediate size, in no case have I observed anything corresponding to Castle's results with rabbits or Lock's results with corn. In every case with which I am acquainted, there has been segregation of size characters in F_2 following a "blend" in F_1 . The cases in which this behavior has been studied most carefully are: size and shape of fruits of summer squashes and gourds, varieties of *Cucurbita pepo*; size and shape of bean seeds, *Phaseolus vulgaris*; size of grains and height of stalks of *Zea mays*.

Size of Maize Grains.—Queen's Golden pop corn, having small grains, was crossed with Black Mexican sweet corn, having grains of medium size. The grains of F_1 plants are intermediate between the parents in size and show no more variation in size than do the grains of the parent plants.⁵ F_2 grains, as regards size, while uniform for any one plant, show marked variation between different plants. The actual measurements can not be reported at this time, but an examination of the material on hand shows that there are some ears with grains fully as large as those of Black Mexican, others with grains quite as small as those of Queen's Golden, still others whose grains are about the size of the F_1

⁵On ears of F_1 plants of this cross there are of course about three smooth starchy grains to one wrinkled, sugary grain. While, on account of "double fecundation," the endosperm, like the embryo, of F_1 plants is to be regarded as F_2 , exhibiting the ordinary F_2 segregation, the size of grains is a plant character and to be regarded as F_1 . The wrinkled grains are apparently of practically the same size as the smooth ones, though there is probably considerable difference in weight between the two lots. In a study of weights, where one parent is sugary and the other starchy, it would be advisable to use only the starchy grains of F_1 plants, and for the sugary parent only starchy, "xenia," grains produced through cross-pollination by the starchy parent. It would doubtless be better, however, to avoid this difficulty by the use of only starchy or only sugary parents.

grains, and finally grains intermediate in size between F_1 and each of the parents. What will happen in F_3 can not be told until this season's crop has been studied.

Height of Maize Stalks.—Tom Thumb pop corn is the smallest variety of maize that has come to my notice and is fully as early as any I have seen. Plants, as grown at Lincoln in 1909 and 1910, averaged about 90 cm. in height, and had on the average about eight nodes. In 1909 they ripened in seventy days from planting. This dwarf early race was crossed with a late dent corn obtained from Missouri. The stalks of the latter are above medium height for dent varieties grown in this section, though in the dry seasons of 1909 and 1910 they have reached an average height of only about 225 cm. The average number of nodes is about nineteen. The plants failed to ripen fully in 1909, owing to late planting, but were within perhaps a week of full maturity at the time of the first frost, 120 days after planting. The F_1 plants, as grown in both 1909 and 1910, are as uniform in height as either parent, with an average height of about 182 cm. (about 25 cm. above mid-parental height) and an average number of nodes of about 12 ($1\frac{1}{2}$ nodes below the mid-parent). In 1909 the F_1 plants ripened in about 100 days from planting (practically the mid-parental season). The F_2 plants (about 250 are now growing) range in size from that of the Tom Thumb parent to above that of the F_1 plants. No plant, however, is so tall as the large dent parent. While records have not as yet been made of heights, number of nodes and earliness in case of all plants, there is apparently little correlation between height and earliness. Some of the earliest plants are above medium height and some of the latest are very short. As to correlation between number of nodes and height and between number of nodes and earliness, nothing can now be said.

Size and Shape of Summer Squashes.—A cross of Yellow Crookneck and White Scallop has been grown, and F_1 and F_2 studied in small numbers. The fruit of

Crookneck has a long neck with a bowl of only medium diameter. Scallop has very flat fruits. F_1 is intermediate in both dimensions and therefore also in shape, *i. e.*, in ratio of length to breadth. F_2 shows a complete series of dimensions and of shapes from one parent to the other. The mean dimensions and shapes and the coefficients of variation in sizes and shapes for parents, F_1 and F_2 are given in the following table.

Race or Hybrid.	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Crookneck	39.6	11.4	3.47	17.0	12.0	13.8
Scallop	7.4	17.8	.41	15.8	12.6	26.8
Mid-parent	23.5	14.6	{ 1.94 ⁸ 1.60 ⁷	16.4	12.3	20.3
F_1 Hybrid	17.5	17.5	1.00	19.0	12.6	26.0
F_2 Hybrid	19.6	13.2	1.48	42.7	42.5	58.8

Size and Shape of Gourds.—A cross of Striped Spoon gourd with Filipino Horned gourd has been studied.⁸ The Spoon gourd has a small, relatively long fruit. The relation of length of the whole fruit to the diameter of the bowl is similar to Crookneck squash. The Horned gourd has a short, relatively thick fruit. The ratio of length to breadth is greater than in case of Scallop squash. The following table gives the mean sizes and shapes and coefficients of variation in size and shape of the parents, F_1 and F_2 .

Race or Hybrid.	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Horned	10.3	9.0	1.14	9.4	9.9	10.9
Spoon	14.0	4.2	3.36	15.6	16.0	11.8
Mid-parent	12.2	6.6	{ 2.25 ⁹ 1.85 ¹⁰	12.5	12.9	11.4
F_1 Hybrid	12.9	5.6	2.27	15.8	15.7	13.4
F_2 Hybrid	15.7	5.5	2.87	37.5	21.2	40.7

⁸ Mean of parent shapes.

⁷ Shape of mid-parent.

⁸ Most of the work with this cross is being done by F. W. Hofmann, a graduate student in plant breeding at the University of Nebraska.

⁹ Mean of parent shapes.

¹⁰ Shape of mid-parent.

Size, Shape and Weight of Bean Seeds.—Numerous crosses of beans differing in size and shape of seeds have been under observation. In only a few cases, however, have exact measurements been made. It will be sufficient to report here combinations of three races: Fillbasket Wax with large flat seeds; Longfellow with long, slender seeds; and Snowflake Navy with small round seeds. The mean dimensions, shapes and weights and the coefficients of variation for parents, F_1 and F_2 , are given in the tables below. The parent races and the F_1 plants from which these records were taken were grown in the garden at Lincoln in 1909. The F_2 plants were grown in a greenhouse during the following winter. The different generations are not, therefore, perfectly comparable. In general the various races of beans and F_1 plants that have been grown from time to time both indoors and out have not been observed to exhibit greater variations when grown in the greenhouse than when grown in the garden, though the dimensions and weights of seeds are often noticeably larger in case of greenhouse-grown plants.

In case of the beans, summer squashes and gourds, the mean dimensions and shapes of both F_1 and F_2 are, with some exceptions, more or less like those of the mid-

MEANS

Race or Hybrid.	Weight, c. g.	Length, mm.	Breadth, mm.	Thickness, mm.	L : B	L : T	B : T
Longfellow	28.3	12.9	5.6	4.6	2.3	2.8	1.2
Snowflake	16.4	8.3	5.7	4.7	1.5	1.8	1.2
Mid-parent	22.4	10.6	5.7	4.7	1.9	2.3	1.2
F_1 Hybrid	18.4	10.1	5.7	4.3	1.8	2.4	1.3
Fillbasket	32.2	13.8	7.6	4.4	1.8	3.2	1.7
Longfellow	28.3	12.9	5.6	4.6	2.3	2.8	1.2
Mid-parent	30.3	13.4	6.6	4.5	2.1	3.0	1.5
F_1 Hybrid	28.4	13.0	6.5	4.7	2.0	2.8	1.4
F_2 Hybrid	36.8	14.1	7.0	5.0	2.0	2.9	1.4
Fillbasket	32.2	13.8	7.6	4.4	1.8	3.2	1.7
Snowflake	16.4	8.3	5.7	4.7	1.5	1.8	1.2
Mid-parent	24.3	11.1	6.7	4.6	1.7	2.5	1.5
F_1 Hybrid	25.4	11.4	6.4	4.5	1.8	2.5	1.4
F_2 Hybrid	28.6	11.3	6.9	4.8	1.6	2.3	1.4

COEFFICIENTS OF VARIATION

Race or Hybrid.	Weight, Per Cent.	Length, Per Cent.	Breadth, Per Cent.	Thickness, Per Cent.	L : B Per Cent.	L : T Per Cent.	B : T Per Cent.
Longfellow	6.09	3.27	3.57	4.54	0.61	1.76	2.46
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	7.75	3.08	3.63	4.96	1.79	3.75	3.28
F ₁ Hybrid	9.19	1.11	2.84	1.69	3.18	4.35	3.73
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Longfellow	6.09	3.27	3.57	4.54	.61	1.76	2.46
Mid-parent	7.01	3.25	2.89	4.16	2.00	3.88	3.16
F ₁ Hybrid	7.63	3.53	1.43	3.37	3.35	2.55	2.95
F ₂ Hybrid	17.43	8.83	10.33	9.45	7.61	12.88	13.10
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	8.67	3.06	2.94	4.58	3.18	5.87	4.07
F ₁ Hybrid	9.90	3.47	2.70	3.83	1.29	5.04	7.06
F ₂ Hybrid	24.48	8.32	5.96	8.95	7.26	39.74	9.01

parents. The most noticeable feature of the records, however, is the coefficient of variation in F₂ as compared with the parents and with F₁. The coefficient of variation is not, on the whole, materially greater for F₁ than for the parents. In F₂, on the contrary, it is noticeably greater than in F₁. It is usually twice and in some cases six or seven times as great as in F₁. This is merely a mathematical way of expressing the fact that the F₂ individuals exhibit marked segregation of size and shape characters. If the intermediates seen in F₁ were tending to breed true as blends, the coefficients of variation for F₂ would not be appreciably greater than for the parents and for F₁. This segregation in F₂ is so pronounced as not to need statistical treatment for its proper appreciation. Even a casual examination of the material can not fail to impress one with the fact that about all grades from one parent to the other are represented in F₂. As a matter of fact, some individuals among the F₂ gourds are decidedly larger than either parent.

If such results as those reported here are to be "explained" by assuming that variation is increased (in some mysterious way?) by hybridization, we can doubtless also explain, in the same way, why this increase in

variation is deferred until F_2 . While predictions can not be made with much assurance before F_3 has been studied, it seems probable, nevertheless, as suggested by East,¹¹ that we shall eventually find that sizes and shapes are not simple characters, but that a particular mean size in reality depends upon two or more, perhaps upon several, distinct factors, a part, or all, of which exhibit incomplete dominance. If this were true, we should expect intermediates (blends) in F_1 and a range of variation from one parent to the other, or sometimes even beyond the parents, in F_2 just as we do find in case of many plant characters. It should also follow that certain F_2 sizes breed true in F_3 while others continue to break up, the variation in some cases extending over the same range as in F_2 and in other cases over variously restricted ranges. There is some evidence that this suggested behavior in F_3 occurs not only in regard to size characters, but also in case of certain colors where blends are seen in F_1 , but observations are as yet too meager to be presented.

I am of course not unmindful of the many chances for mistakes in interpretation of the facts secured in a study of size and shape characters. In the apparently simple cases of height of maize stalks or of bean plants, it must be remembered that parents differing in height may also differ in number of nodes, so that segregation in the latter character might bring about differences in height. Number of nodes and average internode length must both be studied instead of merely the product of these, actual height. Or perhaps, parents can be found that differ in height but have the same number of nodes. Confusion resulting from increased fluctuations due to differences in soil and season can be lessened by growing some plants of all generations to be studied in the same season (from seed kept for the purpose or by repeated crosses), and on as uniform soil as can be had. Even in the same summer plants with different periods of de-

¹¹ East, E. M., *AMER. NAT.*, 44: 72, 73 (1910).

velopment may be subjected to very different weather conditions. This is of so much importance in maize, for instance, that I am now beginning a study of size inheritance of crosses between parents differing greatly in size but only slightly in earliness.

There may possibly be definite correlations between different dimensions, as length and breadth of the same plant part. That is to say, shapes may be definitely inherited. Observations on F_2 bean seeds where the parents differ in size but not in shape indicate that length and breadth are probably not inherited independently of each other. Large round beans crossed with small round ones do not give any long slender beans in F_2 but only large, medium and small, round ones. On the other hand, when the parents differ in shape as well as in size, intermediate and parental shapes as well as intermediate and parental dimensions occur in F_2 .

In short, the inheritance of sizes and shapes is not the simple matter that the inheritance of, say, color is—and recent developments indicate that color inheritance is not always a simple three-to-one affair. It is certainly well that most effort has first been directed to a solution of some of the more simple problems of genetics. Without a knowledge of the later studies in color inheritance, one could scarcely hope to get far in the investigation of the inheritance of dimensions, weights and shapes, to say nothing of such questions as whether “yield Mendelizes,” which some are impatient to have answered at once.

It has been the purpose of this paper to present a few facts and to suggest many problems with the hope that the attention of other students of genetics will be directed to an interesting and important field not much worked as yet.

SHORTER ARTICLES AND DISCUSSION

THE MODIFICATION OF MENDELIAN INHERITANCE BY EXTERNAL CONDITIONS

A WHOLE number of the *Biological Bulletin* (May, 1910) is devoted to Professor W. L. Tower's article on "The Determination of Dominance and the Modification of Behavior in Alternative (Mendelian) Inheritance by Conditions Surrounding or Incident upon the Germ Cells at Fertilization." The work was done on certain chrysomelid beetles, *Leptinotarsa signaticollis*, *L. undecimlineata* and *L. diversa*, all occurring in Mexico. Every biologist who takes any interest in questions of heredity will read this exceedingly important paper, and will be profoundly impressed by the data therein presented, but it is possible that he will also be somewhat puzzled. It is in a humble frame of mind that I venture to set forth some of the difficulties, fully realizing that Professor Tower, with his long experience in patiently investigating the chrysomelid beetles, must know what he is about, and that any mere outsider is at a tremendous disadvantage. At the same time, it is after all for the outsider that the paper is written, and it is due to him to make it as clear as possible, and it may be to explain what seem to him insuperable difficulties.

L. signaticollis ♀ was crossed with *diversa* ♂, giving in F_1 about half *signaticollis* and half a blend between the two. The F_1 *signaticollis* mated together gave only *signaticollis*, and further breeding for five generations gave only the same. The blend, however, split in F_2 into *signaticollis*, the blend, and *diversa*, giving the expected Mendelian ratios. (The obvious suggestion here would be that the original male *diversa* was heterozygous, gametically identical with the blend.)

Next, the same cross was again made, using beetles of the same stock but at a reduced temperature. As a result, the F_1 beetles were of one sort only, the blend; and these, when inbred, gave in F_2 a typical Mendelian grouping. These two crosses were repeated eleven times with substantially the same results.

It is to be noted here that *signaticollis* appears to be a form of lower altitudes than *diversa*, and it seems possible that under

the reduced temperature the pure *signaticollis* perished, leaving only the heterozygous individuals, giving the stated results. Were this the case there would be no real modification of inheritance. So far good, but now we come to the next group of experiments. Another cross was made, *signaticollis* ♀ × *diversa* ♂, under the same conditions as the first experiment, giving the same results. Then the same beetles were used again, at reduced temperatures (as in the second experiment above), and gave in F₁ only *signaticollis*, and this, inbred, continued true for four generations. This experiment was repeated seven times with uniform results. It seems astonishing that the cross in the first set of experiments at a lower temperature should give only the blend, and in the second only *signaticollis*. This, however, is not only explicitly stated, but is illustrated by plates showing the pedigrees of the beetles. In spite of all this there *must* be something wrong, because on page 295 it is stated that the results of the second group of experiments *confirmed* those of the first, and on page 304 it is said that the results of the second were "in every way the duplicate" of those of the first. On page 330 experiment H. 410 (the first group, at the lower temperature) is said to have given beetles exactly like the female parent (*signaticollis*), which subsequently bred true!

Is it possible that the description of H. 410 (p. 294) belonged to something else and was accidentally put in the wrong place when the paper was made up? If so, was the plate then made up from the erroneous description? There is no reason, of course, for doubting the accuracy of the experiments, but certainly there is something wrong with the account of them.

On page 299, in experiment H. 701, there arose a "single pearly white larva [which] gave rise to a female exactly like the parent type and four classes of larvæ." Something has dropped out here, and the statement as it stands is unintelligible.

In experiment H. 700 A (p. 296) a female *undecimlineata* was crossed with a male *signaticollis*, giving *only* the female (*undecimlineata*) type, which bred true for six generations. "The male type was as completely eliminated as if it had never existed." This was not a result of parthenogenesis, as all efforts to induce *undecimlineata* to reproduce parthenogenetically failed. Here it is interesting to note that *undecimlineata* differs principally from *signaticollis* in having fully pigmented bands on the elytra—a positive character. The larva of *undecimlineata*,

however, is white, while that of *signaticollis* is bright yellow—the latter apparently the positive character. In the cross, the larvæ and adults were equally of the *undecimlineata* type, although it was shown in another experiment that the larval and adult characters were inherited independently, each of four classes of larvæ giving rise to three classes of adults, with Mendelian numbers. It was found perfectly possible for *undecimlineata* to have yellow larvæ, and for *signaticollis* to have white ones, when the right crosses had been made.

Are we to explain H. 700 A by saying that the result was a genuine hybrid, from the make-up of which was somehow rejected the superficial characters of *signaticollis*?

Another class of experiments, described as "experiments in synthesis" was productive of extremely interesting results. At Cuernavaca, Mexico, a suitable spot was planted with the proper food-plants, and stocked with 210 specimens of *signaticollis*, "from a standard location about a mile and a half distant" and 354 specimens of *undecimlineata*. These freely bred together, giving in the first generation 4,518 *signaticollis*, 11,744 mid-type, and 5,091 *undecimlineata*. Gradually, however, the *signaticollis* increased at the expense of the others, until at length it was the only form present. This looks like natural selection, and it will be noted that it occurs in a region normally inhabited by *signaticollis*. The experiment seems ideally perfect, except for the stated circumstance that there was a standard locality for *signaticollis* about a mile and a half away. From what we know of the migrations of these beetles,¹ it does not seem unlikely that the colony was overrun with immigrating *signaticollis*.

At Paraiso, in the foot hill rain forest, a locality was planted with 100 each of *signaticollis* and *undecimlineata*. This, I take it, is in the *undecimlineata* country. The result was exactly the reverse of the experiment just described—or not exactly that, for the *signaticollis* practically disappeared even in the first filial generation. Many other particulars are given, and there is an important theoretical discussion, but of course Professor Tower has still in hand a great mass of unpublished material of great value. One may hope that its appearance will not be too long delayed.

T. D. A. COCKERELL.

¹ For example, in six years I had never seen *L. decemlineata* (the potato beetle) in Boulder, Colorado; but this year (1910) it appeared in enormous numbers, flying. The tomato plants in my garden swarmed with them.

NOTES AND LITERATURE

NOTES ON HEREDITY AND EVOLUTION

MENDEL, in his investigations, found certain *Hieracium* hybrids which did not split up in the second generation. The writer several years ago suggested that the cause of this phenomenon might be found in apogamy. Ostenfeld¹ has recently shown that in a large number of species of this genus apogamy exists. It therefore seems probable that the constancy of these hybrids is due to the omission of the reduction division.

Pearl and Surface² have recently published some very interesting contributions on inheritance as a result of studies of crosses made between Barred Plymouth Rock poultry and Cornish Indian Games. It was found that eggs produced by the cross Barred Plymouth Rock males on Cornish Indian Game females gave a larger per cent. of fertile eggs than the reciprocal cross; also a larger per cent. of fertile eggs than either pure breed produced. The low percentage of fertile eggs in the cross in which the Barred Plymouth Rock female was used, the authors suggest, may possibly be due to unfavorable environment for Cornish Indian Game spermatozoa in the Barred Plymouth Rock oviduct.

There was also a higher per cent. of fertile eggs hatched for the hybrids than for either pure breed, this result being attributed to the greater vigor of the hybrids.

The Barred Plymouth Rock breed is one which has high egg-laying quality, while the Cornish Indian Game has low egg-laying quality. The very interesting result was obtained that hybrids produced by using Barred Plymouth Rock sires were good layers, thus showing that the high laying quality was transmitted by the Barred Plymouth Rock sire. On the other hand, hybrids produced by using Barred Plymouth Rock females did not possess the high laying quality, thus indicating

¹Ostenfeld, C. H., "Further Studies on Apogamy and Hybridization of the *Hieracium*," *Zeitsch. f. Induk. Abst.*, Vol. III, H. 4.

²Raymond Pearl and Frank M. Surface, "Studies on Hybrid Poultry," Annual Report, Maine State Experiment Station, 1910. See also *Arch. f. Entwickl. d. Organ.*, XXX, p. 1.

that the Barred Plymouth Rock female does not transmit this quality directly. The facts appear to indicate that high egg laying quality is a sex limited factor like barring in the Barred Plymouth Rocks. Barred Plymouth Rock females would thus transmit high egg laying quality to their male offspring but not to their female offspring, while Barred Plymouth Rock males would transmit it to both sexes.

Shank color was also found to be a sex limited character. Both breeds have yellow shanks, though the Barred Plymouth Rocks sometimes have black pigment in the shank epidermis. In the cross Barred Plymouth Rock male on Cornish Indian Game female the progeny all have yellow shanks. In the reciprocal cross the male progeny have yellow shanks, while the female progeny have black shanks. The authors suggest that shank color behaves like barring in transmission. There is, however, evidently some difference, for here we get females showing a character not possessed by either parent. The writer would suggest, as a possible explanation of the behavior of shank color, that the chromosome which determines the female sex in the Barred Plymouth Rock probably has black shank latent and that this character is aroused into activity by the cross. The F_2 generation of this cross will probably give some important information on this point. Fortunately, these careful and indefatigable workers will continue these investigations.

In down color the hybrid chicks from the reciprocal crosses were alike but unlike either parent, being darker than the darkest parent.

The F_1 generation between pea comb (Cornish Indian Game) and single comb (Barred Plymouth Rock) gave all gradations from pea to single. There were more pea combs in some families than in others.

In body shape the males in the F_1 generation were all of the Cornish Indian Game type. The females were intermediate between the two breeds in this respect. The barred females—that is, those produced from Barred Plymouth Rock sires—were more like the Barred Plymouth Rock in body shape, and the black females more like the Cornish Indian Game.

In this paper the authors give the results of extended investigations relating to inheritance of the Plymouth Rock Barring. The paper is limited to the study of the cross between Barred Plymouth Rocks and Cornish Indian Games. The results con-

firm the present writer's hypothesis first published in 1908³ concerning the method of inheritance of this character. The results obtained are consistent with the hypothesis that barring is allelomorphic to the female sex element. Thus, when male Plymouth Rocks are used in the cross only the male offspring are barred, the females being black. The plates accompanying the text show excellent illustrations of the nature of the barring, both in the pure bred Barred Rocks and in the hybrids. The hybrids are darker than the pure breeds, there being more pigment in the feathers.

Davenport has recently published an important contribution in the Carnegie Institution series on inheritance in poultry.⁴ While he deals with many other characters than those relating to color, for lack of time to present an adequate review of the whole article, and because of its relation to the present subject, I give here only his results relating to color factors. The factors determined were as follows:

C = presence of color (absence of C gives albinism);

J = Jungle Fowl pattern and coloration;

N = super Melanic factor (nigrum);

X = super Xanthic or buff factor;

W = Graying (white) factor.

He found the Silkies and White Cochins both to be pure albinos having the gametic formula $cJnwx$.

White Leghorns were found to be grays with the formula $CJNWx$. This formula shows that W is an inhibiting factor which renders J and N invisible.

Black Minorcas and white-faced Black Spanish were found to have the formula $CJNwx$. In these breeds N obscures J, but the latter modifies the character black color.

Black Cochins were found to have the formula $CINwx$. In this formula I is a modification of J in which the pigmentation usually associated with J is absent.

Black Games were found to have the same formula as Black Cochins, but the pigment due to the factor N is less intense.

Buff Cochins were found to have the formula $CjnwX$. The author notes some variability in the degree of albinism, certain recessive whites showing specks of pigment. "The coloring enzyme may be absent to small traces."

³ AMERICAN NATURALIST, Vol. 42, 1909, pp. 610-615.

⁴ Davenport, C. B., "Inheritance of Character in Domestic Fowls," Carnegie Institution publication.

While the author recognizes sexual dimorphism as related to Jungle Fowl pattern, he does not work out the manner of inheritance of this factor. He probably would have done so had the birds been raised to the stage required for distinguishing this dimorphism.

Breeders of White Leghorns are frequently troubled by the appearance of a reddish sheen on the feathers. The formula of this breed gives a probable reason for this difficulty (CJNWx). It is probable that the Jungle Fowl coloration produces the effect in question. The cross between this breed and the Buff Cochin (CjnwX) gives an opportunity to get a breed of the formula CjnWx, which ought to be a pure dominant white, with no trace of coloration or pigment.

Goodale⁵ has recently published a short but very interesting paper giving results of poultry breeding experiments, in which it appears that the Jungle Fowl pattern found in the Brown Leghorns, like the barring factor of the Barred Plymouth Rocks, is allelomorphic to the female sex factor. His paper also shows that while dominant white, when homozygote, is epistatic to black pigment, it is not so in the heterozygote condition of the white. It also indicates that females possessing the Jungle Fowl pattern and having Plymouth Rock white and Plymouth Rock black pigment, both in the heterozygote condition, may vary in color from black to almost typical Brown Leghorn pattern.

The progeny of females obtained by mating Brown Leghorn females with white Plymouth Rock males show no trace of the Jungle Fowl pattern or color, while the males obtained from this cross transmitted the Jungle Fowl pattern. There is opportunity here for a very interesting study. If the Jungle Fowl pattern and the barring of the Plymouth Rocks are both allelomorphic to the female sex factor, it would be very interesting to ascertain whether females can have both of these factors present in them. If so, it would show either that the female sex factor itself may be coupled with one or the other of these factors, or that the allelomorph to this factor may contain both factors coupled, or that the two factors reside in separate chromosomes both of which behave as allelomorphs to the female sex chromosome.

Castle has recently shown⁶ that Miss McCracken's results in

⁵ *Proc. Soc. Exp. Biol. and Med.*, Vol. 7, No. 5, May 18, 1910.

⁶ Castle, W. E., *Jour. of Exp. Zool.*, Vol. 8, No. 2, March, 1910.

univoltinism and bivoltinism⁷ are not inconsistent with Mendelian theory. The difficulty in interpretation is due to the fact that the characters in question are exhibited by one sex only. The same difficulty arises in following out the cross between white and red corn, since red shows only as an internal character.

Hagedoorn,⁸ in mating an albino mouse having the barring (agouti) character with a homozygous yellow female, finds the barring and the yellow color to be allelomorphic to each other. Certain yellow individuals mated to black gave only yellow offspring. It is probable that the yellow contains an inhibiting factor for black. Other yellow mice of a different shade mated to black gave black young. His results confirm those of Goodale in that he finds the bankiva pattern and color in Bantams crossed with Brown Reds to behave as if the bankiva pattern were allelomorphic to femaleness. When females of the bankiva type were used in the cross the male offspring were all bankiva and the females all Brown Red. When the cross was made in the opposite direction both sexes were of bankiva type. He also found (page 26) some bankiva females apparently homozygous for bankiva pattern. His data are not full or complete on this point.

On page 29 he reports that the cross between *Primula sinensis* and *P. stellata* gives *P. pyramidalis*. F₂ from this cross gives 25 per cent. *sinensis*, 25 per cent. *stellata*, and 50 per cent. *Pyramidalis*, although the two parent forms differ in more than one respect, the differences apparently being coupled.

The writer has frequently suggested that if a careful search were made for more cases of what Bateson has termed "false allelomorphs" they might be found to be more abundant than they are thought to be. Those cases which have been discovered show that such phenomena are not discovered usually unless one is looking for them. We have now a considerable number of cases of sexual dimorphism in which some somatic character acts as an allelomorph to femaleness. Presumably, these sex-limited characters would act as allelomorphs to each other if brought together in the same zygote. We have already referred to the barring of Plymouth Rocks and to the Jungle

⁷ *Jour. of Exp. Zool.*, Vol. 7, No. 4.

⁸ Hagedoorn, A. L., "Mendelian Inheritance," *Arch. f. Entw. d. Organ.* Vol. 28, H. 1.

Fowl pattern as instances of this kind. When Silkies are crossed with Brown Leghorns, the latter breed introduces an inhibiting factor for the intense black pigmentation in the flesh of the Silkies, and this inhibiting factor appears to behave as if it were allelomorphic to femaleness. The inheritance of the factor is not yet fully worked out.⁹ In addition to these cases we have that of melanism in *Abraxas grossulariata* when crossed with *A. lacticolor*. Black eyes in canaries when crossed with pink eyes appear to behave in a similar manner. We have already mentioned above shank color in poultry in this connection.

Dr. R. A. Gortner, of the Station for Experimental Evolution, Cold Spring Harbor, New York, in THE AMERICAN NATURALIST for August, 1910, gives results of quantitative determinations of melanin in white wool and black. He finds 1.84 per cent. in black wool and only .06 per cent. in white. He expresses the opinion that the melanin in white is a decomposition product of keratin and not a true melanin, thus disproving Riddle's assumption that dominant white is a more advanced stage of oxidation than black. He advances the theory that dominant whites are due to the presence of an anti-oxidase which prevents pigment formation, while recessive whites have neither power to form pigments nor to inhibit the formation.

Ostenfeld¹⁰ finds that the number of chromosomes in the apogamic race of *Rosa canina* is about double the number in the normal sexual race in the same species, thus indicating that the reduction division is omitted.

It has generally been supposed that when an organism is moved from one environment to another distinctly different, there is a tendency for the type to break up. This thing has been described as "new place effect." There has been very little investigation bearing directly on this question, and most of it has related to forms more or less mixed in inheritance rather than to pure lines of the same inheritance. Data bearing on this subject are important and very much needed. An important contribution to our knowledge of the subject is found in Bulletin 128 of the Bureau of Chemistry of the U. S. Department of Agriculture. In this bulletin LeClerc and Leavitt give the results of experiments on wheat. Kubanka Wheat grown

⁹"Bateson's Mendelian Principles of Heredity," pp. 81-87.

¹⁰Zeitsch. f. Induk. Abst. und Vererb., Bd. III, H. 4, May, 1910, p. 253.

in South Dakota was distributed to stations in Kansas and California. Each year a sample from each station was sent to each of the others and grown there. A similar series of experiments was conducted with Crimean Wheat in Kansas, Texas and California. The results may be briefly stated as follows.

The same variety of wheat when grown at the same station, no matter what the source of the seed, showed the same characteristics, but the same variety grown at different stations showed marked differences. This result was obtained in the case of both varieties. These results are in entire accord with the results on barley secured by Dr. Albert Mann, who grew pedigree seeds of barley at a large number of stations in this country. The original seed was from Svalöf. These results have been previously referred to in these notes.

The appearance of an English edition of de Vries's "The Mutation Theory" (Vol. I)¹¹ gives the opportunity for many non-German readers to gain first hand knowledge of this remarkable work. It also serves to show the truly wonderful progress that has been made in the study of the phenomena of evolution since this book was originally published (1901-03).

In reading this book one can not fail to be impressed with the current misconceptions concerning its teachings. De Vries's disciples have given the phrase "discontinuous variation" a meaning quite different from that in which it is used in "The Mutation Theory." By "continuous" variability de Vries means the kind that fluctuates about a norm and thus presents a continuous series of modifications. Illustrations of continuous variability in this sense are found in ordinary fluctuating variations within pure lines. It was Quetelet who first discovered the fact that ordinary fluctuating variability gives a continuous series of variations varying in frequency inversely with their magnitude. That is, the magnitude of a given variation of this kind is governed by the ordinary laws of probability. In such variation every degree of departure from the normal is found. On the other hand, if we study a given character in a complex Linnean species consisting of several pure strains or subspecies, we find that each of the pure strains gives us a case of continuous variation—i. e., of "fluctuation" about a norm which is fixed. But if we take these norms for a large number of pure

¹¹ de Vries, Hugo, "The Mutation Theory," Vol. I, The Open Court Publishing Co., Chicago, Ill., pp. 575.

strains within a species and attempt to arrange them in a frequency polygon, we find gaps not represented in the series, at least in some species. This kind of variation de Vries calls "discontinuous variation." We can all agree that there are such gaps between related forms in many cases. Thus, if we adhere to the original use of the term "discontinuous variation," there is no chance for debate about it. It is simply a name given to a series of well ascertained facts. How these gaps came into existence is another question. The change in the use of the term which has occurred since "The Mutation Theory" was written is in its application to the method by which these gaps came to exist rather than to the fact of their existence.

A careful consideration of the data now at hand seems to the writer to leave little question that there are gaps between related forms which came into existence suddenly, and thus represent discontinuous variation in the more modern sense of this term. The only dispute which seems to the writer justifiable relates to the question whether all permanent evolutionary change comes about in this manner; and this question will be brought up again later in this article.

The progress made since "The Mutation Theory" was published is illustrated by the fact that in this book de Vries takes no account of the pure lines differing quantitatively with reference to a given character, such as those studied by Jennings, Johannsen, Nilsson-Ehle and others. De Vries also adheres throughout the book to the old notion that a given character can be modified quantitatively by selection, and states on page 51 that "It is to the selection of the material afforded by individual variability [fluctuation] that the origin of many improved races is due." Many other similar statements occur in the text. Recent investigations have thrown much doubt on the correctness of this view; we may say, have disproved it. All the recent careful work on the subject points to the opposite conclusion.

While in this book de Vries sets forth very clearly the idea that his "individual variation" is what we now call fluctuation, he continually confuses fluctuation with the effect of crossing. For instance, on page 100, we find the following: "All this [improvement of the sugar beet] has been done by selection of the best individuals afforded by ordinary fluctuating variation. Neither spontaneous variations nor crossings have played any

part in it. We are dealing here with the process in its simplest form." It is far from demonstrated that crossings have had nothing to do with the improvement of the sugar beet. The consensus of opinion of most biologists at the present time is that selection can accomplish nothing except the isolation of the best strain or best Mendelian combination existing in a given population. It is hardly fair, however, to attribute to de Vries the opinions expressed ten years ago, for he would probably hold to-day that the opinions expressed concerning the effect of selection in "The Mutation Theory" have been proved to be incorrect. Such a position is really more in keeping with the fundamental principles involved in his theory, and I have no doubt that de Vries would fully admit that selection can not affect fluctuating variability, or at least that all of the recent evidence points in this direction.

For the purpose of discussing de Vries's fundamental theorem we may classify the various types of variation as follows: (1) Fluctuation; (2) those due to Mendelian recombinations; (3) those due to change in personnel of the chromosomes or other cell organs having a relation to ontogenetic development; (4) those due to fundamental changes in whatever material is responsible for the metabolic activities which result in development.

Fortunately, at the time "The Mutation Theory" was written the general facts of Mendelian recombination were recognized and are taken into account by de Vries, though, as previously stated, he frequently confuses them with other types of variation. De Vries also recognizes fluctuation, which he describes by the term "individual variability," and appraises it at its true value, except, as stated above, that he credits selection with the power of producing temporary modifications by means of it.

The last two types of variability were not recognized when "The Mutation Theory" was written, so that they are utterly confused in this book.

Before de Vries undertook his *Oenothera* studies he was already committed to a theory concerning the manner in which evolutionary changes come about, and frankly states that his work was undertaken in order to find confirmation of this theory. Strangely enough, Darwin was responsible for the fundamental idea underlying de Vries's theory of mutation. It will be remembered that in attempting to explain the sup-

posed inheritance of acquired characters Darwin formulated the theory of pangenesis, according to which each cell in the organism gives off a bud, or gemmule, which migrates to the germ plasm and in the next generation becomes responsible for the development of a corresponding cell in the new organism. De Vries drops the idea of migration of the gemmules from the organism into the germ plasm, and starts with these gemmules as permanent constituents of the germ plasm. He also makes other modifications in the nature of these bodies, and hence very properly gives them a new name, "pangenes."

I am of opinion that had de Vries taken an agricultural variety of wheat for his studies he would have been led to the development of a different theory. Unfortunately, he found the mutations for which he was looking in a species which was throwing off variants in a manner which we may well believe to be unusual. In fact, de Vries examined over a hundred species before he found one that suited him in this respect. Recent cytological investigations by Gates, Miss Lutz and others seem to justify at least the tentative assumption that the *Oenothera* mutants arise from a change in the personnel of the chromosomes. It is certain that in *Oenothera gigas* the *Lamarckiana* the number of chromosomes has been doubled. Gates has shown that in a general way the nuclei in *gigas* cells are twice the size of those of *Lamarckiana*. Other mutants have numbers of chromosomes not exactly corresponding with *Lamarckiana*. It is also demonstrated that in *Lamarckiana* and several of its mutants the course of events in the reduction division is abnormal. A good many of the chromosomes do not unite into bivalents in the usual manner, thus giving opportunity for all kinds of irregularities in the distribution of the chromosomes. The further fact that many of the mutants produce only a small proportion of functional gametes at least suggests that in many reduction divisions the chromosomes are distributed in such a way as to interfere with the future development of the gametes and the zygotes which would be formed from them.

If we assume that the chromosomes, because of their relation to the processes of nutrition or for other reasons, have an important influence on the course of development, and that there are irregularities in the distribution of these bodies in the reduction division in *Lamarckiana* and its offshoots, we at once find a satisfactory interpretation of the behavior of these mu-

tants, and we can easily see how de Vries was misled by his material. He got the idea that the organism is composed of distinct and independently heritable units and that when one of these units is lost out or when a new one springs into existence we get an organism which differs in all of its characters from the parent form. He assumes that all permanent evolutionary change comes about by the introduction of new pangenesis. For instance, he says:

The contrast between these two groups of phenomena, variability (in the strict sense) [fluctuation] and mutability, becomes obvious when we imagine that properties of organisms are built up of perfectly distinct and independent units. The origin of a new unit is a mutation.

Again on page 57:

Elementary species and forms closely allied to them are distinguished from one another not by a single feature but by all their organs and peculiarities. The difference between closely allied forms often demands long and extensive diagnosis. Nevertheless this diagnosis must be regarded as an expression of a single character, a single unit, which arose as such, and as such can be lost.

Again, on Page 61: "By mutation new characters arise all at once"; and on page 63: "Each mutation is a definitely circumscribed unit."

De Vries overlooks entirely those closely related pure lines, differing frequently only quantitatively, and in a single character, which to the writer represent what may be called normal evolutionary change. They not only do not differ in all their characters as the *Oenothera* mutants do, but their norms present a regular series coming under Quetelet's law, and thus represent "continuous variation," as de Vries defines it. Yet they are undoubtedly of true evolutionary value. Of these types Jennings says:¹²

The work with genotypes [pure lines] brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurement taken in connection with statistical treatment.

And again on page 145:

That smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements. Genotypes

¹² AMER. NAT., XLIV, pp. 144-145.

so differing have not risen from each other by large mutations. The genotype work lends no support to the idea that evolution occurs by large steps, for it reveals a *continuous series*¹³ of the minutest differences between great numbers of existing races.

Nilsson-Ehle, in dealing with genotypes of oats, shows that the related lines can be arranged in a Quetelet curve with respect to the average length of the flowering glume,¹⁴ as follows:

Average length of hull mm.	Number of genotypes
14-15	2
15-16	16
16-17	38
17-18	14
18-19	2

It would be difficult to imagine a better case of "continuous variation," as defined by de Vries.

To the writer it seems there can be no doubt that the type of variation illustrated by these pure lines of oats, and by the many pure lines of *Paramecium* studied by Jennings, is altogether different from that studied by de Vries, and is due to a widely different cause. In the writer's opinion, the *Oenothera* mutants are due to irregularities in the distribution of chromosomes in the reduction division, while the hereditary variations of the *Paramecium* type are due to actual changes in function (increase, decrease) of cell organs that have a relation to development. When such changes occur in the functions of chromosomes, the resulting differences obey Mendel's law; when they occur in other cell organs they do not obey this law.

De Vries simply generalized from too small a range of phenomena. There can be very little doubt that had he worked with the numerous small differences that exist in many species, such as have been the subject of later studies by others, he would have come to a different conclusion, or would have at least greatly modified his conclusions. The work with genotypes certainly points to a different cause for evolutionary change from that assigned by de Vries. Had he recognized what we may call the *Paramecium* type of mutation he certainly would not have said (p. 155):

The assumption that human variability bears any relation to the variation that has or is supposed to have caused the origin of species

¹³ Italics mine.

¹⁴ *Bot. Not.*, 1907, pp. 113-140.

is to my mind absolutely unjustified. . . . Since the beginning of the diluvial period man has not given rise to any new races or types. He is, in fact, immutable, albeit highly variable.

But even those of us who do not believe that *all* evolutionary change is saltatory, as it seems to be in the *Oenothera* mutants, can agree with de Vries that the difference between fluctuation and mutation lies in the fact that fluctuation is due to environment and is not hereditary, while, when a step has actually been accomplished in permanent evolutionary change, the norm about which fluctuation occurs is different from the old one. We can accept this doctrine even if we deny that the difference between the new and the old is not a "unit." We can not, however, accept the idea, repeatedly brought forward in this book, that "There is no question that improvement takes place in the experimental garden" (p. 110) when selecting for improvement in pure lines, or when he says "In the case of no single character can selection be relaxed" (p. 106); or when he quotes Halley (p. 111), with approval, to the effect that in improving wheat by selection, "the rate of improvement gradually falls off year by year until at the end of many years the race reaches a maximum and becomes constant. But, of course, it will not remain so if it is not subjected to continuous selection."

W. J. SPILLMAN.

(To be continued.)

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